

FURTHER STUDIES ON MONOTROPOIDEAE

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This paper continues a series (5, 6, 7, 8, 9), of which the account of *Sarcodes* by Doyel and Goss (12) is to be considered a unit. It records observations on *Pterospora*, *Hypopitys*, and *Monotropa*, and adds to the previous account of *Hemitomes* (*Newberrya*).

It has been a pleasure to acknowledge from time to time the unstinted cooperation of various institutions and individual correspondents. The following have facilitated the preparation of the present contribution: the Herbarium of the University of California; the Dudley Herbarium of Stanford University; the Herbarium of the California Academy of Sciences; Dr. W. L. Jepson; Mr. Willman Spawn; Dr. W. H. Camp; Dr. P. L. Zimmerman; and the Oregon Biological Supply Company.

PTEROSPORA ANDROMEDEA Nuttall

Pterospora andromedeae was described by Nuttall (25) as collected "In Upper Canada, near the Falls of Niagara. Mr. C. Whitlow." There has been essentially no nomenclatorial confusion as to this plant; no segregation of species or varieties has been proposed; Small (28) cites a single obscure synonym. The plant is common in the mountain ranges of western North America; rare eastward to the region of the type locality.

The material studied was collected from time to time at Jonesville, Butte County, California, at an altitude of about five thousand feet. There the plant shares the habitat of *Sarcodes* and *Pleuricospora*, in forests of fir (*Abies concolor*). As compared with its congeners, *Pterospora* emerges from the ground and flowers noticeably later in the season; it is usually in full anthesis late in July.

The shoots come up from globular masses of roots. It is noticeable that whereas they emerge in the neighborhood of dead shoots of the previous year, they are not in immediate contact with such dead shoots, nor at a distance to be measured in centimeters, but a meter or more away. Jepson (19) believes that the plant is monocarpic, and it is probable that he is correct. There is, however, the possibility that the scattered shoots come up from long roots which have emerged from the masses. This is suggested by the behavior of the generality of monotropoid plants, in which the genetic individuals are polycarpic, forming shoots year after year as adventitious buds on the same root system. A positive determination of this matter could be attained only by determining the course of individual roots in a mass of humus, and I have not undertaken it.

The standard accounts of the gross structure of the shoot, as by Jepson and Small, leave essentially nothing to add. The tall and slender stems, densely glandular, are of a light purplish red color. The greater part of each shoot is a rather lax bracted raceme, usually but not always exhibiting orthodox phyllotaxy. The recurved glandular pedicels bear no bractlets. The five glandular sepals are separate. The five petals form a glabrous sympetalous urceolate corolla, yellowish in color, becoming chartaceous in age. Each of the ten stamens bears two horns on the back of the anther. The globular ovary is belted at the base by a nectary from which ten evenly spaced lobes project between the bases of the filaments. Internally, the ovary is five-chambered below, one-chambered above, filled by massive placentae bearing numerous ovules. The stigma is obscurely five-lobed, the lobes opposite the petals, that is, at the ends of the carpels.

MacDougal has described the anatomy of the vegetative parts. The stem includes a cylinder of bundles so closely packed as almost to be continuous; around this there is a well developed continuous sheath of fibers.

The vascular supply of the flower (pl. 8, fig. 1) enters the receptacle as a cylinder. From this there depart radially, first, five sepal bundles, and then, alternating with them, five petal bundles. There are no gaps above these bundles. Five stamen bundles arise as branches from the upper sides of the petal bundles. Above the departure of the petal bundles the stele breaks up into a ring of ten bundles. Of these, the five which are opposite the sepals bend outward and fork periclinally; the outer branches constitute the supply to the five remaining stamens; the inner ascend the ovary wall in the planes of the septa, and are to be interpreted as fused pairs of lateral bundles of adjacent carpels. The five remaining bundles enter the ovary in the planes of the locules, being the planes of the petals and carpels; each of them is a fused pair of ventral bundles of a single carpel. They branch out into the placentae and disappear. In several features the vascular system just described is peculiar. No other monotropoid plant is known to be without carpel dorsals (though they are not well differentiated from carpel laterals in *Sarcodes*); in none do the placental bundles lie in the planes of the petals. Here it is as though the proper placental bundles had swung outward into the ovary wall, and the carpel dorsals inward, into the placentae. In most plants of the group, the style is supplied by the carpel dorsals, which ascend in the thin bands of tissue between the ridges projecting into the style channel. *Sarcodes* is exceptional in that the placental bundles supply the style, ascending within the ridges. In *Pterospora*, lacking carpel dorsals and having the placentals in a peculiar position, the style is without vascular tissue.

As is known, the anther (pl. 8, figs. 2-7) projects horizontally toward the style from the summit of the filament, and bears two

horns, inserted respectively on the two sides of the insertion of the filament and projecting toward its base. A vascular bundle runs from the summit of the filament to the inward end of the anther; by this it is known that the inward end is distal, the end bearing the horns proximal, the upper side dorsal, and the lower side ventral. There are four parallel horizontal pollen sacs; the dorsal ones are larger than the ventral. A cross section shows the epidermal cells extended into conical points on the dorsal and ventral, but not the lateral, surfaces. Between the epidermis and the tapetum there are some two or three layers of wall cells; near the horns a few of these cells develop reticulate lignified thickenings, as in the endothecium of a typical flowering plant. A similar structure has been reported in *Sarcodes*, and will be reported below in *Monotropa*; it is less extensive in *Pterospora* than in these other genera, being apparently merely a relic structure. The cells of the tapetum become binucleate. The pollen grains are four-grooved.

Dehiscence of the anther begins by two vertical slits, each of which crosses the proximal ends of the two pollen sacs of one lobe of the anther. Formation of these slits amounts to the same thing as the dehiscence of the anthers of *Sarcodes* or *Monotropsis*, being, as I take it, the typical dehiscence of the anthers of Ericales. Subsequently two secondary slits develop from the middles and at right angles to the primary ones, that is, in the plane between the two pollen sacs of each lobe of the anther. By a general shrivelling of the walls of the anther, accompanied by growth of the connective, these secondary slits gape widely; it is through them that most of the pollen escapes. Drude's (13) figure of the fully dehisced anther is accurate, though it gives a false impression that the connective becomes torn in a horizontal plane from proximal to distal.

The internal surface of the ovary wall is covered by two layers of well developed fiber-like cells.

A complete series of stages of the development of the seed has not been seen, and there is nothing to add to my earlier notes (4). The embryogeny appears to be altogether typical of the group. The integument is of two layers of cells. The wing on the seed is of two layers of cells. It commences to form, by proliferation of the epidermis of the integument at the chalazal end, before the embryo sac is fully developed.

HYPOPITYS MONOTROPA Crantz

Only two species of monotropoid plants were known to Linnaeus (23). One, known in English as the pine-sap, occurs on all continents of the north temperate zone; the other, the Indian pipe, occurs in North America and eastern Asia, but not in western Asia and Europe. The oldest Latin designation of the pine-sap seems to be *Orobanche quae hypopithis dici potest*, of Bauhin (1671). It is of course no *Orobanche*; Tournefort (1706)

gave it as name the adjective *Orobanchoides*; Dillenius (1719) took up the substantive designation recorded by Bauhin, as *Hypopitys*. The Indian pipe, first recorded by Plukenet (1671) under *Orobanche*, was named *Monotropa* by Gronovius (about 1740). Linnaeus included both species in one genus, for which he used the name *Monotropa*, the species becoming respectively *M. Hypopithys* and *M. uniflora*. The breach of priority as to the generic name was immediately protested by Hill (16): "Linnaeus takes away its received name *hypopitys* and calls it *monotropa*." Because he was the first after 1753 to use *Hypopitys* as the name of a genus, Hill is cited as authority for it; this in spite of the facts, that he did not originate it, and that he did not use binomials and cannot be cited as authority for any of the species. Binomials under *Hypopitys*¹ were first made by Crantz (10), the pine-sap becoming *H. Monotropa* and the Indian pipe *H. uniflora*.

Inasmuch as the first post-Linnaean authors gave to *Hypopitys* exactly the extent which Linnaeus had given to *Monotropa*, it might be held that the two names are exact synonyms, and that *Hypopitys* is not available as the name of any genus. On the other hand, the pre-Linnaean history shows that the two names are based on different types, and that if the pine-sap is placed in a different genus from the Indian pipe its name is *Hypopitys*. Such in effect was the conclusion of the pre-type-system authors Nuttall (25) and Bentham and Hooker (1); such was the conclusion of Small (27), who made the combination *Hypopithys Hypopithys*. Repeating binomials being excluded by our rules, we must accept the first specific epithet published after 1753; this yields, as has been shown, the combination *Hypopitys Monotropa*. We might be glad to reject this combination as a matter of taste; it has gone almost completely unaccepted since its original publication; but the rules are designed to spare us the responsibility for a choice.

I follow Kamienski (21) and Domin (11; this work has been a most valuable guide to the history and literature) in recognizing only one species of *Hypopitys*. There are considerable variations, and Small (28) has recognized five species in North America alone; but these variations seem so inconstant as to make the recognition even of varieties a critical matter.

The available material preserved in liquid has included several roots, stems, and flowers collected by Dr. W. H. Camp, in Oregon, Ohio, and Tennessee, and two shoots with nearly ripe fruit collected by Mr. Willman Spawn in Rock Creek Park, Washington, D. C., in July of 1938.

¹ Variations in the spelling will be noted. I have not consulted the pre-Linnaean publications. Linnaeus wrote *Hypopithys*, Hill and Crantz *Hypopitys*. These are mere variant spellings; but we are forbidden by rule to meddle with them. In using the word as a specific epithet, we must follow Linnaeus; in using it as a generic name, we must follow Hill.

Nothing is here added to knowledge of the gross structure. The shoots originate endogenously in roots, a mass of which constitutes the permanent organ of the plant. Domin, after a long discussion of the literature, concludes that the underground structures are not true roots, but an axis not differentiated as root or stem, to be called the *Prokaulom* (anglicizable as *procaulon*). I have not examined these structures, but the conclusion is inescapable, from Kamienski's (20, 21) description and from what is known of the other monotropoid plants, that Domin is mistaken. As Christoph (3) has shown, the occasional more or less complete suppression of some of the characters of roots—the cap and endogenous branching—depends on the presence of mycorrhiza. The same effacement of character appears in the roots of other plants when they are beset with mycorrhiza.

The shoot is usually yellowish and more or less pubescent. The upper part of it constitutes a bracted raceme. When it emerges from the ground, the raceme is bent to one side, and the buds or flowers are crowded and more or less pendant; later the axis and pedicels become erect and the flowers or fruits become separated. At its maximum the shoot is rarely twenty-five centimeters tall.

The lateral flowers (pl. 8, fig. 8) stand in the axils of bracts whose margins vary from entire to lacerate. There are no bractlets; four sepals, a lower pair placed laterally and an upper pair placed dorsally and ventrally with regard to the flower; four separate petals with saccate bases, alternating with the sepals; eight stamens; a nectary with eight horn-like lobes arranged in pairs which clasp the bases of the petalad stamens; a pistil, the ovary four-chambered below, one-chambered above, the stigma obscurely lobed, the lobes opposite the petals. Variations in the proportions of ovary and style, as well as in color, pubescence, and the indentation of the margins of the bracts, have been utilized for subdivision of the species.

Older accounts definitely described the terminal flower as pentamerous. I have not found such a flower. I believe that in the few shoots preserved in liquid which I have examined the terminal flower has been suppressed. The highest flower has been tetramerous, the pedicel embraced by two bracts instead of one (evidently as a result of shortening of the last internode, the one above the insertion of the flower), the lower pair of sepals somewhat removed from the flower.

Domin cites many authors who have disagreed as to whether the outer envelope of the flower is really a calyx, and its segments sepals: Eichler is the chief authority in the affirmative, Baillon in the negative. He quotes observations of Irmisch (17) and Wydler (30) and gives his own, to the effect (a) that the upper pair of leaves of this envelope are, one or both of them, often suppressed; (b) that the lower pair are often somewhat withdrawn from the base of the flower; (c) that these leaves, espe-

cially the lower pair, often have buds in their axils. He concludes that they are not true sepals, but elevated bractlets in process of conversion into sepals. It seems to me unreasonable to recognize a calyx in course of coming into existence in any group as advanced as Ericales: rather, any irregularities are to be interpreted as matters of degeneration. Since *Allotropia* is the only positively asepalous genus of the monotropoid group; since only *Monotropis* and sometimes *Allotropia* have definite bractlets; we may interpret the facts assembled by Domin in some such fashion as this: the structures of *Hypopitys* now under consideration are positively sepals; they are affected by a tendency to degeneration; it is possible that a tendency to produce bractlets, almost completely extinct in this genus, retains enough strength to affect the course of the degeneration.

Kamienski has accounted in full for the anatomy of the vegetative parts; I have here only to describe the vascular supply to the flower. One bundle from the circle in the stem turns outward. It becomes flattened tangentially and presently splits into three branches, of which the middle one supplies the bract while the two on the sides swing together and unite as a cylinder ascending the pedicel. All this is quite the same as in the genera previously studied. The cylinder of vascular tissue ascending the pedicel becomes compressed in the dorso-ventral plane, so as to approximate a four-sided prism (pl. 9, fig. 10). From each of its faces there departs a sepal trace, leaving a small gap or none. The traces to the lateral sepals depart at a much lower level than those to the dorsal and ventral sepals; this is in harmony with Domin's observations as to the relative positions of the sepals. The petal bundles emerge as broad bands from the angles of the prism; each promptly forks into three, of which the one in the middle is the smallest and descends under the sac of the petal, while the larger lateral ones ascend past the sac. The petalad stamen bundles are not fused with the petal bundles, but are closely associated with them; each originates as a pair of bundles at the sides of a petal bundle, the pair drawing together and uniting above the petal bundle. The sepalad stamen bundles emerge at the edges of the siphonostele as it breaks up. The carpel dorsals, well developed in the ovary walls and style, are only with difficulty traced to their origin; the feebly developed provascular strands that lead into them seem to originate typically as paired strands beside, above, and resembling the petalad stamen bundles. Foster (15) has recently quoted Gregoire to the effect that floral

EXPLANATION OF THE FIGURES. PLATE 8.

PLATE 8. PTEROSPORA ANDROMEDEA. FIG. 1. Model of the vascular system in the receptacle $\times 50$. *Ca*, sepal bundles; *Co*, petal bundles; *St*, stamen bundles; *Cl*, carpel laterals; *Pl*, placental bundles. FIGS. 2, 3. Juvenile stamens, $\times 10$. FIG. 4. Longitudinal section of juvenile stamen, $\times 50$. FIG. 5. Cross section of juvenile stamen at the plane marked *x* in fig. 4, $\times 50$. FIG. 6. Area marked *x* in fig. 5, $\times 400$. FIG. 7. Cross section of dehisced stamen, $\times 50$. HYPOPITYS MONOTROPA. FIG. 8. Old flower in which the fruit is nearly ripe, $\times 5$.

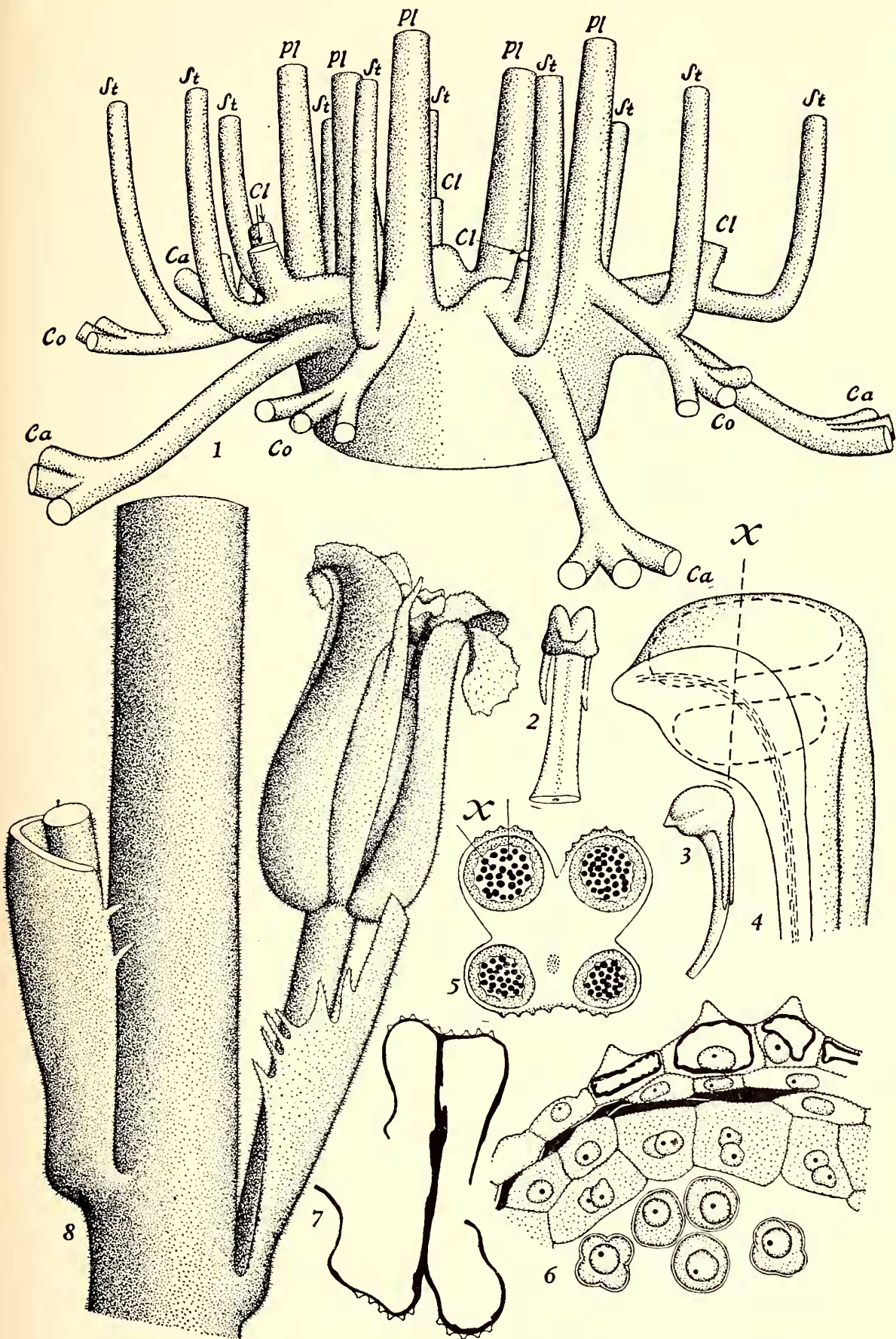


PLATE 8. PTEROSPORA ANDROMEDEA; HYPOPITYS MONOTROPA

leaves are distinguished from vegetative leaves by acropetal development of the vascular supply. The carpel dorsals of *Hypopitys* (and likewise, as will be seen, of *Monotropa* and *Hemitomes*) constitute an exception to this principle. The breaking up of the siphonostele finally yields one bundle to each lateral placenta, and two each to the dorsal and ventral placentae. This seems to be an outcome of the bilateral character of the whole vascular system. It is as though the ventral bundles of adjacent carpels were fused at the sides of the flower, but not at the front and back.

It is regretted that no anatomical study has been made of young stamens. The anther opens by two vertical slits at the outer, presumably proximal, end; these slits meet above, separating a small outer valve from a large inner one; and soon the valves liberate the pollen by swinging widely apart. Young stages and old ones (pl. 9, figs. 11, 12) respectively agree exactly with corresponding stages of *Pityopus* as illustrated by Eastwood (14). It is particularly regretted that the position of the pollen sacs was not ascertained; though it may be presumed that there are four in each anther, lying horizontally, each slit of the anther crossing the ends of two of them. The pollen grains are two-grooved.

The fruit is a capsule, its inner surface covered by a single layer of elongate cells not distinguished by staining reactions.

The development of the seed has been described in detail by Koch (22). I have seen only one stage, conforming well to Koch's account, and so beautifully clear that I could not refrain from drawing it (pl. 9, fig. 9).

MONOTROPA UNIFLORA L.

Of the name of this genus and species enough has been said above. The genus is apparently monotypic; no variation even of varietal rank is recognized as occurring within the United States. *Monotropa coccinea* Zuccarini, of Mexico and Central America, and *M. australis* Andres, of Colombia, were treated as varieties by Domin.

The available material preserved in liquid has included six collections, as follows: (1) Three shoots purchased some years ago from the New York Biological Supply Company, as a museum specimen, without collection data. (2) Three shoots presented by the Oregon Biological Supply Company; collected by R. E. Griffin, Bullrun, Oregon, July 11, 1939. The fluid preserves the white color of the plants, and makes specimens excellent for museum use rather than for sectioning. (3) A number of shoots presented by the Herbarium of the University of California, without collection data. (4) One shoot, with roots, furnished by Mr. Willman Spawn; collected in Rock Creek Park, Washington, D. C., July, 1938. (5) One shoot, with roots, furnished by Dr. P. W. Zimmerman; collected in the arboretum of the Boyce Thompson Institute for Plant Research, New York, summer, 1939.

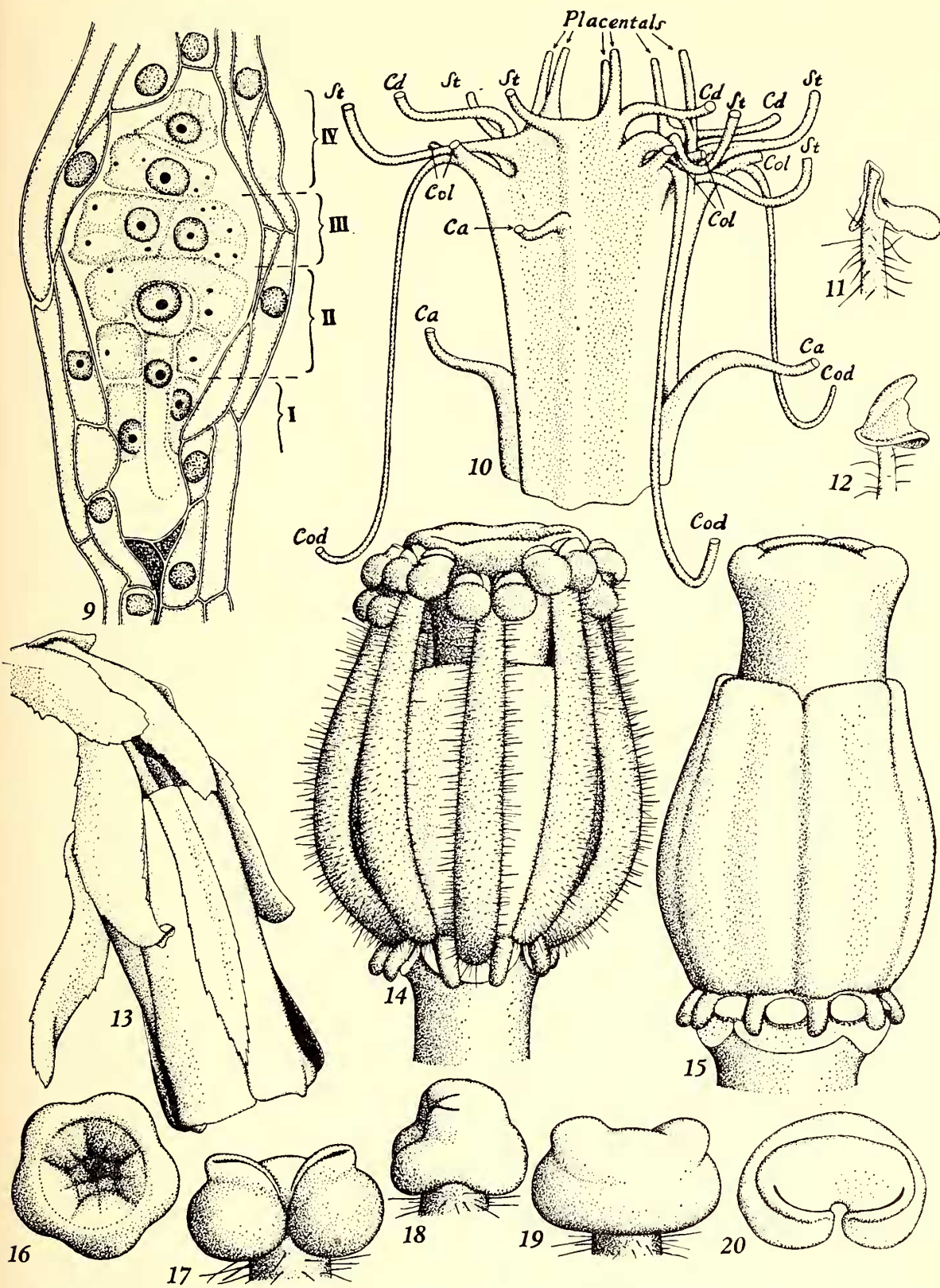


PLATE 9. *HYPOPITYS MONOTROPA*. FIG. 9. Longitudinal section of nearly ripe seed $\times 400$. The endosperm, at a certain early stage, is four-celled; the Roman numerals I-IV indicate the derivatives of these cells. FIG. 10. Model of the vascular system in the receptacle $\times 12.5$: *Ca*, sepal bundles; *Cod*, petal dorsals; *Col*, petal laterals; *St*, stamen bundles; *Cd*, carpel dorsals. FIGS. 11, 12. Dehiscent anthers $\times 10$. *MONOTROPA UNIFLORA*. FIG. 13. Flower $\times 2.5$. FIG. 14. Flower with perianth removed $\times 5$. FIG. 15. Pistil $\times 5$. FIG. 16. Stigma $\times 5$. FIGS. 17-20. Anthers $\times 10$.

(6) Roots, shoots, flowers and fruits furnished by Dr. W. H. Camp; collected in central New York State at various times.

As is well known, the erect shoots are in life white, like paraffin (the austral races mentioned above are distinguished by red color); dried, or placed in most preservatives, they turn black. The stem is clad with spiral scales; study of a single example showed the spiral to be orthodox. The solitary flower (pl. 9, fig. 13) is terminal on the recurved summit of the stem. Domin has quoted many conflicting authorities as to whether or not sepals are present. I find that a varying number of scales may project past the base of the flower. Of these, sometimes none and sometimes one is inserted so immediately below the petals that it can be regarded as a sepal. It is not particularly different from the leaves, and I have not found more than one. The five separate petals overlap at the margins so as to form a campanulate corolla about fifteen millimeters long. Each petal is saccate at the base and truncate at the apex, sometimes with an apiculation. There are ten stamens, manifestly in two whorls, the lower opposite the petals. The densely pubescent filaments are curved inward and bear the subglobular anthers pressed against the lower side of the stigma (pl. 9, fig. 14). The ovary is belted at the base by a ten-lobed nectary; the lobes are cylindrical; they are obscurely but perceptibly paired, clasping the bases of the petalad stamens. The ovary is ovoid, marked by five deep longitudinal grooves opposite the petals, that is, in the median planes of the carpels; and by five shallow grooves between them where the carpels meet (pl. 9, fig. 15). A shallow circular depression at the summit of the ovary is filled by the base of the short, stout, obconical style. The stigma is five-lobed, the lobes opposite the petals and surrounding an unusually large crater-like depression which leads into the style passage. The depression is lined by five masses of tissue which stand above the grooves, not the ridges, in the style passage. The surfaces of the five masses of tissue are more or less wrinkled, and the grooves in the style passage are obscurely continued upward upon them to some distance (pl. 9, fig. 16).

The stem resembles in its anatomy that of *Pterospora* rather than those of *Monotropsis* and *Hypopitys*. It shows in cross section a ring of separate strands of xylem and phloem (in most specimens seriously shattered by shrinkage, apparently during fixation, a difficulty commonly encountered also in *Sarcodes* and *Pterospora*). Around the cylinder of bundles there is a continuous sheath of pericyclic cells with thinly lignified walls, being imperfectly developed fibers.

At the summit of the stem the sheath disappears. Exactly ten bundles enter the receptacle (pl. 10, fig. 25). Each of the five lying in the planes of the petals breaks up, typically, into five. Of these, the middle one is the petal bundle; it forks further into three, a small petal dorsal which follows the contour of the sac, and two larger petal laterals which ascend past it. The behavior

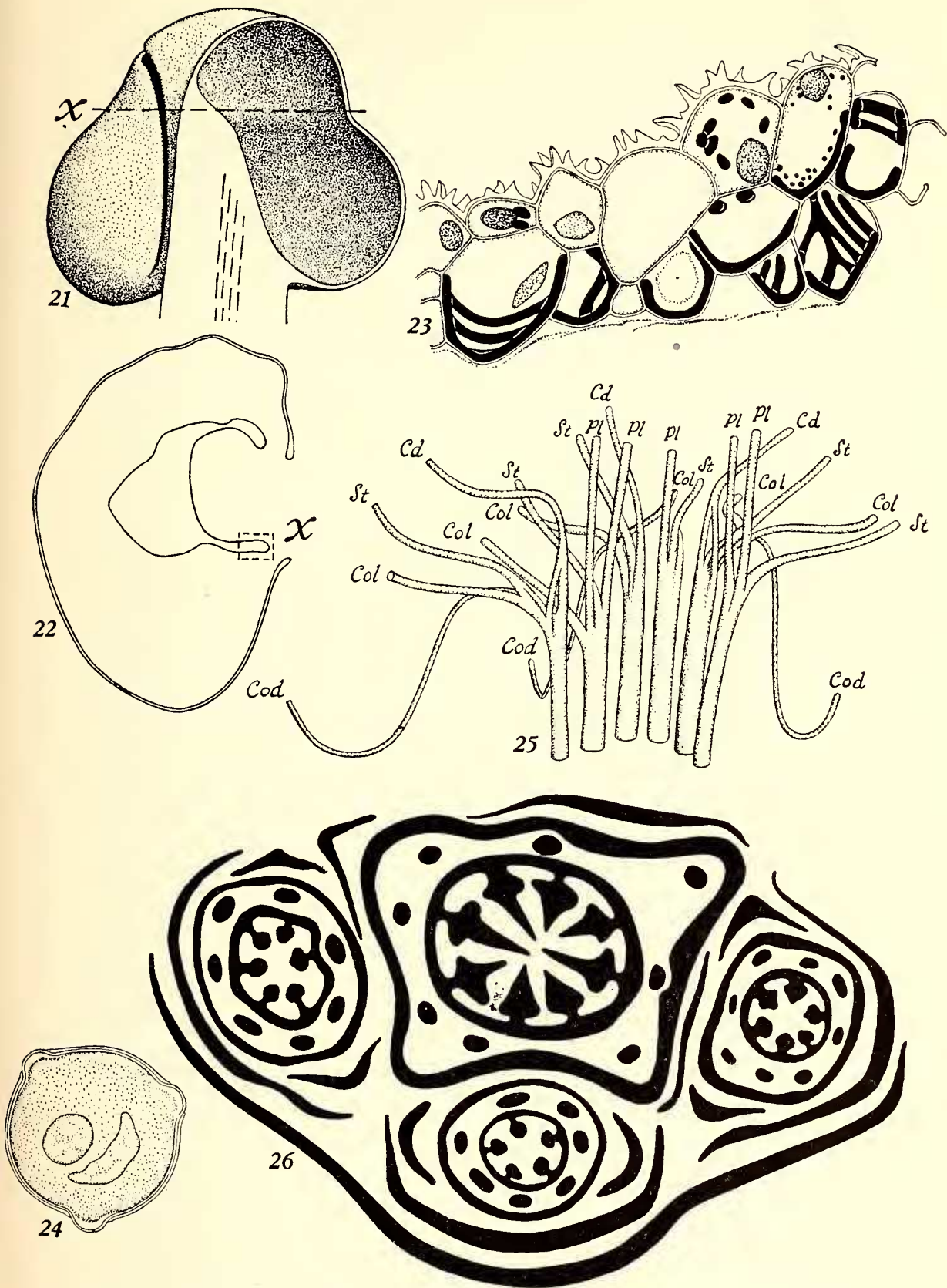


PLATE 10. *MONOTROPA UNIFLORA*. FIG. 21. Longitudinal section of anther $\times 25$. FIG. 22. Cross section of anther at the plane indicated by *x* in fig. 21 $\times 25$. FIG. 23. Area marked X in fig. 22 $\times 400$. FIG. 24. Pollen grain $\times 900$. FIG. 25. Model of half of the vascular system in the receptacle $\times 12.5$: *Cod*, petal dorsals; *Col*, petal laterals; *St*, stamen bundles; *Cd*, carpel dorsals; *Pl*, placental bundles. *HEMITOMES CONGESTUM*. FIG. 26. Cross section of primary flower with three secondary flowers in the axils of the sepals $\times 10$.

of these petal bundles is quite the same as in *Monotropsis*, *Hypopitys*, and *Pityopus*. The two bundles adjacent to the petal bundle unite above it to form a petalad stamen bundle, and the two marginal branches unite to form a carpel dorsal which is traced with difficulty here at its origin. As to the five bundles which enter the receptacle between the planes of the petals, each of these forks into three: the middle one supplies a stamen of the upper whorl; the lateral ones enter the placentae, being ventral bundles of adjacent carpels. The figure shows minor deviations from the assumed typical structure as just described: one of the petal lateral bundles does not originate from a proper petal bundle; one of the placental bundles is suppressed. The carpel dorsals enter the style and ascend it for some distance, but they are there poorly developed.

If the anther (pl. 9, figs. 17–20; pl. 10, figs. 21–23) is correctly understood, the outer end is proximal, the inner distal, the upper side dorsal and the lower ventral. At anthesis it includes a single chamber. Apparently (these points were regrettably not established) there are in the juvenile anther four horizontal pollen sacs, of which the ventral pair are much the larger. Dehiscence is through two curving slits at the proximal end; in dried material, and doubtless in life, these slits flare open as gaping pores. Along the margins of the slits the anther walls, elsewhere of one layer of collapsed cells, are of two layers, the walls of the inner layer bearing reticulate lignified thickenings as in a normal endothecium (pl. 10, fig. 23). Jepson states that the slits eventually meet, so as to convert the anther wall into two valves. This is not true in such fruiting material as I have seen; on the contrary, the pores retain their individuality until the plant dies and decays. The pollen grains (pl. 10, fig. 24) are three-grooved. The tube nucleus stains poorly and becomes distorted; the generative nucleus remains globular and deeply staining, and is surrounded by a clear space (not shown in the figure), the generative cell.

The inner surface of the ovary wall is covered by a single layer of somewhat elongate cells not distinguished by staining reactions.

Of the stages in the development of seed, we know only the structure of the mature ovule. It was described and figured long since by Campbell (2) quite as in *Hypopitys*.²

² Since the above was written Dr. Zimmerman has had the kindness to send a beautiful collection of fruiting material made in the Arboretum of the Boyce Thompson Institute in late summer of 1940. The seeds are much as in *Allotropa*; they are elongate, having a tail at each end; the embryo, borne on a suspensor, is usually of two cells; the endosperm has a haustorium at each end. It is now known that haustoria are produced on the endosperm in *Sarcodes*, *Allotropa*, *Monotropa*, and probably (to reinterpret a former observation) in *Monotropsis*; and that they are not produced in *Hypopitys* and *Pleuricospora*. I suppose that the absence of haustoria in these two genera is a result of parallel evolution and that the classification given at the end of this paper, in which *Hypopitys* falls near *Monotropa* and *Monotropsis* and far from *Pleuricospora*, may stand.

HEMITOMES CONGESTUM Gray

Under the name of *Newberrya*, I have given a partial description of this rather uncommon plant of the Pacific Coast of North America, and have quoted from Jepson; but Jepson's description and mine require extension and amendment.

The original generic name *Hemitomes* was rejected by Torrey (29) as inappropriate; and the rejection was maintained by Small (28) on account of the priority of *Hemitomus* L'Her. Torrey's objection is of no standing in modern nomenclature; and Small's is disposed of by the rule (26) "When the difference between two generic names lies in the termination, these names must be regarded as distinct, even though differing by one letter only." Small recognized five species. Jepson has reduced three of these, whose type localities are in California, to synonymy with the type species. With this I fully agree, and I add the one which Jepson omitted as outside his area. I am glad to remark that Professor John Davidson has tended to support this action, in a paper read at Seattle in June, 1936; and that Dr. W. H. Camp has done so in private correspondence. The synonymy, then, is as follows:

Hemitomes congestum A. Gray, Pacif. Rail. Rep. 6: 80. 1857. *Newberrya congesta* Torr. in Gray, Bot. Calif. 1: 464. 1876. *N. spicata* A. Gray, Proc. Am. Acad. 15: 44. 1879. *Hemitomes pumilum* Greene, Erythea 2: 121. 1894. *Newberrya subterranea* Eastw., Proc. Calif. Acad. Sci., ser. 3, 1: 80. 1897. *Hemitomes spicatum* Heller, Cat. No. Amer. Pl. 5. 1898. *H. subterraneum* Heller, *op. cit.* *Newberrya longiloba* Small, No. Amer. Fl. 29: 18. 1914. *N. pumila* Small, *op. cit.*

The Herbarium of the University of California has a photograph of the type of *Newberrya spicata*, and a photograph and a duplicate of *Suksdorf 2168*, the type of *N. longiloba*. I have been particularly helped by Dr. Jepson, who loaned a specimen collected by W. G. Wright, the type of *H. pumilum*. Two collections preserved in liquid have been available: (1) One shoot without roots, furnished by Dr. L. R. Abrams, who collected it in the California State Redwood Park, Santa Cruz County, June 14, 1934. (2) Several shoots and roots collected by Dr. W. H. Camp at Sol Duc Hot Springs, in the Olympic Peninsula, Washington, August 5, 1932.

Shoots, arising endogenously from roots, vary in height, the flowers being borne approximately at ground level; they expand in ascending, when well developed exceeding two centimeters in diameter at the base of the inflorescence. The inflorescence is essentially a bracted spike, often so brief and compact as to be accounted a head; in Abrams' specimen the phyllotaxy, both of the leaves below the inflorescence and of the flowers, is orthodox, the apparent divergence being $3/8$ or $5/13$. Depauperate shoots may bear a single flower; on the other hand, vigorous shoots may bear axillary branches with one or more flowers, and may develop

secondary flowers in the axils of the sepals of the primary flowers. This behavior was noted on dissection of the type of *H. pumilum*; of Abrams' specimen; and of a specimen by C. A. Reed in the Herbarium of the California Academy of Sciences. Jepson's words, "Inflorescence . . . composed of short 2- to 5-flowered spikelets" imply that it is normal; but I find it only in a minority of the specimens; I do not find it in Camp's preserved material. The flowers (pl. 11, fig. 27) are practically always tetramerous; the four sepals are oriented as in *Hypopitys* and *Pleuricospora*, dorsally, ventrally, and laterally, the dorsal and ventral sepals being not infrequently suppressed. The sympetalous corolla is variable in length, from less than one centimeter to nearly two centimeters long. The four lobes alternate with the sepals, and are separate to a depth of more or less than one-third the total length of the corolla. The dried corolla is very fragile, and it is hard to be certain as to how deep the sinuses extend. *Newberrya longiloba* was distinguished by particularly deep sinuses, but I do not find these in our duplicate of the type. Indentation of the corolla lobes is variable; the retuse apex mentioned in my former account was merely the character of an individual. Stamens are normally eight, anthers dehiscing by two lengthwise slits on the outside; lobes of the nectary moderately prominent, evenly spaced; carpels eight, alternating with the perianth parts and stamens, so that the parietal placentae, and the lobes of the stigma, standing above them, are opposite the stamens and perianth parts.

Secondary flowers are usually in the axils of the lateral sepals, but may appear also in the axils of dorsal and ventral sepals (pl. 10, fig. 26). In the cluster figured, there is a second pair of scales, like sepals, above the lateral secondary flowers, as if the scales subtending these were bractlets: *Hemitomes* would have afforded Domin even better evidence than did *Hypopitys*, that the outer floral envelope is no true calyx. But what is the scale in whose axil is the dorsal secondary flower? And what is the scale on the ventral side of the primary flower, if not a sepal? I regard the scales subtending the lateral secondary flowers as sepals; and the scales above these flowers as a secondary pair of sepals, anomalously developed in connection with the anomaly of buds in the axils of the primary pair. The secondary flowers ordinarily have parts in smaller numbers than the primary ones, as two sepals, seven or six stamens, seven, six, or five carpels. They are later in development than the primary flowers.

The vascular system in the stem, as reconstructed from sections of Abrams' specimen (pl. 11, fig. 30), is a cylinder interrupted by very large leaf gaps; as there are no other gaps than these, and as the vascular tissue runs in broad oblique bands rather than in slender vertical bundles, it may be regarded as a siphonostele. The leaf traces, emerging at the bases of the gaps, fork into three as they enter the scales. Flower traces are not at all united with the traces to the subtending scales; the supply to

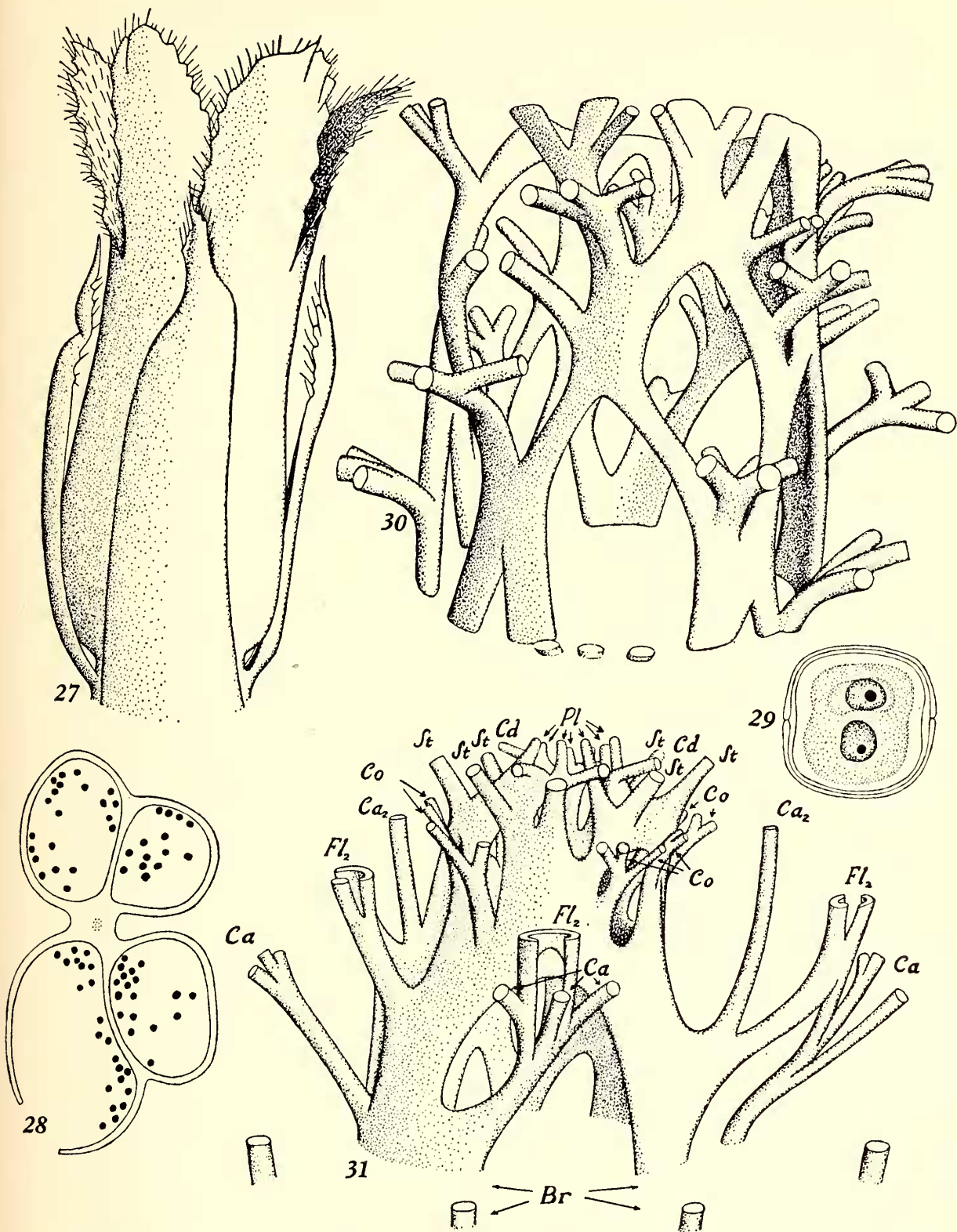


PLATE 11. HEMITOMES CONGESTUM. FIG. 27. Flower $\times 5$. FIG. 28. Cross section of juvenile stamen $\times 50$. FIG. 29. Pollen grain $\times 900$. FIG. 30. Model of the vascular system in the stem $\times 5$. FIG. 31. Model of the vascular system of the cluster of flowers shown in fig. 26 $\times 15$: *Br*, bundles to the bract; *Ca*, sepal bundles; *Fl₂*, supplies to secondary flowers; *Ca₂*, secondary sepal bundles; *Co*, petal bundles; *St*, stamen bundles; *Cd*, carpel dorsals; *Pl*, placental bundles.

each flower consists of two bundles springing from the sides of the gap above one of the upper leaves.

The figure of the vascular system of a primary flower with its attached secondary flowers (pl. 11, fig. 31) was constructed from a series of sections of Abrams' specimen, one of which yielded the diagram (pl. 10, fig. 26). The two bundles of the flower trace approach one another, become flattened, and unite as a siphonostele. Before this union is complete, four sepal traces emerge as single bundles above which there are large gaps. It seems that a secondary flower is typically supplied, like a primary flower, by two bundles springing from the sides of the gap left by the supply to the subtending leaf, which is in this case a sepal. Actually, we find that the secondary flower placed on the left in the figures is supplied as just described; the one on the right is partially so supplied, and partially from the sepal trace; the third, the dorsal secondary flower, is supplied entirely from the trace to the subtending sepal. The single bundles to the secondary sepals of the primary flower arise next to two of the secondary flower bundles. Each petal is supplied by two bundles which leave a single gap in the stele. Beyond these the stele emits three whorls each of eight bundles: stamen bundles, one opposite each perianth segment, all apparently in one whorl, not at all associated with the petal bundles; carpel dorsals, alternating with the stamen bundles, very poorly developed at the base, so that formerly I failed to discover their origin; and placental bundles, opposite the stamen bundles.

Juvenile stamens were found in the secondary flowers. The anther is borne vertically on the summit of the filament and includes four parallel vertical pollen sacs, of which the two on the dorsal side are much the larger. (I was formerly mistaken in making the ventral sacs the larger.) Dehiscence is through vertical slits on the dorsal sides of the dorsal sacs; the wall between the two pollen sacs of each lobe breaks down, and the whole outer wall swings around to the ventral side of the anther as a broad valve.

The cells of the inner surface of the ovary wall are not differentiated except perhaps by smaller size.

No new observations have been made upon the development of seeds; all that is known is that the ovules are essentially like those of *Hypopitys* and other members of the group.

DISCUSSION

In concluding the previous paper of this series, I put forward a tentative scheme of classification of the plants construed as constituting the subfamily Monotropoideae of family Ericaceae:

Tribe Pterosporeae: *Pterospora*, *Sarcodes*, *Allotropa*.

Tribe Monotropeae: *Monotropsis*, *Hypopitys*, *Pityopus*, *Monotropa*, *Monotropastrum*, *Wirtgenia*?

Tribe Pleuricosporeae: *Pleuricospora*, *Newberrya*, *Cheilotheca*?

Observations have now been extended to all of the above-named genera which are native in North America. Not a few of my previous statements have been found to require correction. A summary of the observations constitutes a formidably extensive table (Table 1). The data there assembled enable one to construct a tentative phylogenetic tree (text fig. 1) and to reconsider the proposed scheme of classification.



FIG. 1. Apparent phylogeny of the Monotropoideae.

Pterospora, *Sarcodes*, and *Allotropa* continue to appear more primitive than the other genera. The primitive features are tall and erect habit; bright coloration; axile placentation in the lower part of the ovary; evenly spaced lobes of the nectary; corolla sympetalous, urceolate (in *Pterospora* and *Sarcodes*); bractlets present (in some specimens of *Allotropa* only); anthers horned (in *Pterospora* only); anthers not permanently erect. The only single characters which separate these genera as a group from the others are the habit and the coloration; but the combination of characters, lobes of the nectary not paired and anthers not erect, is also distinctive. In all this, there is nothing to raise doubt as to the status of the tribe Pterosporeae as a natural group; often a primitive group can be distinguished from several derived groups taken together only by a combination of negative characters. Doubt appears when, on the other hand, we compare these genera with the supposed ancestral group *Arbutoideae*. The primitive characters of the Pterosporeae are in large part merely the characters of *Arbutoideae*; only saprophytism and the habit

TABLE 1. CHARACTERS OF NORTH AMERICAN MONOTROPOIDEAE

Genus	Habit	Color	Flower	Placentation	Lobing of stigma	Fruit	Inner surface of ovary	Stele in stem
<i>Pterospora</i> ..	tall, erect	pale purplish red	5-merous sympetalous	axile below, parietal above	obscure; opposite petals	loculicidal capsule	two layers of fiber-like cells	ring of bundles with lignified sheath
<i>Sarcodes</i>	stout, erect, moderately tall	red	5-merous sympetalous	axile below, parietal above	opposite petals	capsule opening about base of style	scant differentiation near line of dehiscence	cylinder without sheath
<i>Allotropa</i> ...	tall, erect	white with red stripes	5-merous choripetalous asepalous	axile below, parietal above	opposite petals	loculicidal capsule	one layer of fiber-like cells	cylinder with sheath
<i>Monotropis</i> ..	slender, rather short, declined when young	white ?	5-merous sympetalous	parietal	obscure	berry	one layer of non-lignified elongate cells	ring of bundles, no sheath
<i>Hypopitys</i> ...	slender, rather short, declined when young	white to yellow	4-merous choripetalous	axile below, parietal above	opposite petals	loculicidal capsule	one layer of non-lignified elongate cells	ring of bundles, no sheath
<i>Pityopus</i>	slender, rather short, erect	white	4-merous choripetalous	parietal	obscure	berry?	undifferentiated	cylinder without sheath
<i>Monotropa</i> ..	slender, rather short, declined when young	white	5-merous choripetalous	axile below, parietal above	opposite petals	loculicidal capsule	one layer of non-lignified elongate cells	ring of bundles with lignified sheath
<i>Pleuricospora</i>	small, erect, flowering at ground level	white	4-merous choripetalous	parietal	opposite sepals	berry	undifferentiated	cylinder without sheath
<i>Hemitomes</i> ..	small, erect, flowering at ground level	pale yellow-pink	4-merous sympetalous	parietal	opposite sepals, petals, and stamens	berry?	undifferentiated	cylinder without sheath

TABLE 1, CONTINUED

Genus	Stele in pedicel and receptacle	Stamen bundles	Ovary wall bundles	Placentals	Style bundles	Anthers and pollen sacs	Dehiscence of anthers	Number of grooves on pollen grains
<i>Pterospora</i> . . .	cylinder	outer whorl fused to petal bundles, inner to carpel laterals	carpel laterals	in planes of petals; each is fused ventrals of same carpel	none	horizontal; dorsal sacs are longer	(1) proximal ends of lobes; (2) lengthwise of sides of lobes	4
<i>Sarcodes</i>	ring of about 5 bundles	outer whorl fused to petal bundles, inner to ovary wall bundles	numerous; no definite carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	placentals	inverted; dorsal sacs are longer	proximal ends of lobes	4
<i>Allotropa</i> . . .	cylinder	outer whorl fused to petal bundles, inner free	carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	carpel dorsals	erect when young, inverted when mature; dorsal and ventral sacs subequal	proximal ends of lobes	3
<i>Monotropis</i> . . .	about 4 partially fused bundles	two whorls, free of other bundles	carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	carpel dorsals	horizontal when young, mature inverted; dorsal and ventral sacs subequal	proximal ends of lobes	2
<i>Hypopitys</i> . . .	flattened cylinder	two whorls, free of other bundles	carpel dorsals	in planes of sepals; fused or unfused ventrals of adjacent carpels	carpel dorsals	horizontal, ventrals sacs longer?	proximal ends of lobes?	2

TABLE I, CONCLUDED

Genus	Stele in pedicel and receptacle	Stamen bundles	Ovary wall bundles	Placentals	Style bundles	Anthers and pollen sacs	Dehiscence of anthers	Number of grooves on pollen grains
<i>Pityopus</i>	cylinder	two whorls, inner connected to pistil bundles	8 carpel dorsals alternating with stamens	8, in planes of stamens	carpel dorsals	horizontal, ventral sacs longer?	proximal ends of lobes?	2
<i>Monotropa</i>	ring of ten bundles	two whorls, free of other bundles	carpel dorsals	in planes of sepals; unfused ventrals of adjacent carpels	carpel dorsals	horizontal, ventral sacs longer?	proximal ends of lobes?	3
<i>Pleuricospora</i>	cylinder	outer whorl fused to petal bundles, inner free	carpel dorsals	in planes of sepals; each is fused ventrals of adjacent carpels	carpel dorsals	vertical, dorsal and ventral sacs subequal	lengthwise of sides of lobes	4
<i>Hemitomes</i>	broken cylinder	apparently one whorl; free of other bundles	8 carpels dorsals alternating with stamens	8, in planes of stamens	carpel dorsals	apparently vertical, dorsal sacs broader	dorsal sides of dorsal sacs	2

which is presumably a result of it are distinctive. Furthermore, the Pterosporeae are notably heterogeneous in anatomy of stem and receptacle, and in corolla, anther, fruit, and seed. I would allow the tribe to stand as a tentative group, and would expect studies of the Arbutoideae to afford evidence as to whether or not it is a natural group, having one origin among Arbutoideae.

The Monotropeae, though differing among themselves in various features, yet exhibit marks of unity; the saccate bases of the petals and the paired lobes of the nectary are associated with a peculiar and definite structure of the vascular supply to the petal. This is safely a natural group. In the corolla, *Monotropsis* is the most primitive of the genera; but in the ovary, *Hypopitys* and *Monotropa* are more primitive, and the feebly developed sheath of fibers is a primitive character in the stem of *Monotropa*. We may take it that in most respects *Monotropsis* represents a direct ancestor of *Hypopitys*, and *Pityopus* an only slightly modified descendant; *Monotropa* stands apart from all three, differing not only in the well known solitary flower and in the anatomy of the stem, but also in the number of grooves on the pollen grain. We may safely maintain *Hypopitys* and *Monotropa* as separate genera.

The tribe Pleuricosporeae has ceased to be tenable as constituted. The common characters of *Pleuricospora* and *Hemitomes*, in habit, floral diagram, placentation, and ovules, are features all of which are apparently readily reached by parallel change and some of which are widely distributed. They are outweighed by the differences in pubescence, vascular anatomy of the receptacle, and structure of the anther.

Pleuricospora is strictly glabrous. The petal bundles, not forking into two large bundles and one small one, are those of Pterosporeae rather than of Monotropeae. The anther is unique; the only thing elsewhere in the group that suggests it is that of *Pterospora*. The four-grooved pollen grains again suggest Pterosporeae rather than Monotropeae. But we cannot connect this genus with any one genus of Pterosporeae.

Hemitomes has the floral diagram of *Hypopitys*, and, in more extreme form, the irregularity of inflorescence observed in that genus. We may account for the unique petal trace of two bundles by supposing the small middle bundle of the petal traces of the Monotropeae to have been suppressed, this suppression being associated with loss of saccate bases to the petals and pairing of the lobes of the nectary. The slits along the dorsal sides of the dorsal sacs of the anthers seem to amount to a modification of the pores of normal Ericales, which are still present in *Monotropsis* and *Monotropa*. The two-grooved pollen grains are those of most Monotropeae.

It would be possible to dispose of these genera by assigning one to Pterosporeae, the other to Monotropeae, distinguishing these tribes by glabrous stamens and pistils in the former, pubescent stamens and pistils in most of the latter. Such a scheme,

however, would increase the heterogeneity of the Pterosporeae and break the unity of the Monotropeae. I think it best to place each of these genera in a separate tribe, making altogether four tribes to be distinguished as follows (the oriental genus *Cheilotheca* remains unplaced; it may perhaps constitute a fifth tribe):

- A. Stamens and pistils glabrous; lobes of the nectary not paired; no gaps above the petal bundles, to which the outer whorl of stamen bundles are more or less fused; grooves on the pollen grain 4 (3 in *Allotropia*); young stems not nodding.
1. Stems erect above ground; red pigment present; anther bent inward; placentation axile below: Tribe PTEROSPOREAE: *Pterospora*, *Sarcodes*, *Allotropia*.
 2. Inflorescence at ground level; red pigment absent; anthers erect; placentation parietal: Tribe PLEURICOSPOREAE: *Pleuricospora*.
- B. Stamens and pistil often pubescent; red pigment usually absent (present in varieties of *Monotropa*, a trace of it in *Hemitomes*); gaps present above the petal bundles; grooves on the pollen grain 2 (3 in *Monotropa*).
1. Bases of petals saccate; lobes of the nectary in pairs; petals with small dorsal bundles and large lateral bundles; young stems nodding (unknown in *Pityopus*): Tribe MONOTROPEAE: *Monotropsis*, *Hypopitys*, *Pityopus*, *Monotropa*, *Monotropastrum*, *Wirtgenia*?
 2. Base of petals not saccate; lobes of the nectary evenly distributed; dorsal bundles of the petals suppressed; inflorescence at ground level: Tribe HEMITOMEAE: *Hemitomes*.

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PODOCARPUS GRACILIOR IN CULTIVATION

JOHN T. BUCHHOLZ

The "African fern-pine," in recent years popular as a decorative tub plant and also planted in the open as an ornamental conifer, may become a tree of considerable size. Since mature specimens growing in California have produced pollen cones during the past winter, it is now possible to identify the species as *Podocarpus gracilior* Pilger.

The plant has been regarded as a conifer of South African origin and has usually passed under the nursery trade name of "Podocarpus elongata," which is unquestionably an error. The latter is the legitimate name of a plant of South Africa where there are two narrow leaved species that have been confused and have at one time or another passed under this botanical name. The California exotic has narrow leaves that are somewhat similar to those of *Podocarpus elongatus* L'Herit. (the earliest described